

COMMUNITY ECOLOGY AND *PIERIS*—CRUCIFER
COEVOLUTION^{1,2}

F. S. Chew

The association of certain subfamilies of Lepidoptera with certain families of flowering plants whose members are exploited as larval food is well known (e.g. Ehrlich and Raven, 1965; Fraenkel, 1959; Whittaker and Feeny, 1971). Among the Pierinae, for example, larvae of the genus *Pieris* are confined to the Cruciferae, Capparidaceae, and a small number of other plant families whose members contain glucosinolates (mustard oil glucosides; Ettliger and Kjaer, 1968). A number of glucosinolates, tested under laboratory conditions, appear to mediate specificity in these plant-insect associations by eliciting feeding and oviposition responses from various *Pieris* (e.g. David and Gardiner, 1966; Hovanitz and Chang, 1963) as well as from other crucivorous species (e.g. Thorsteinson, 1953; Tanton, 1965; Hicks, 1974). In addition, allylthiocyanate, the volatile hydrolysis product resulting from enzymatic degradation of allylglucosinolate (sinigrin) when crucifer tissues are damaged, acts as an attractant to *Pieris rapae* and some chrysomelid beetles (Blau et al., 1978; Feeny et al., 1970; Matsumoto, 1970). Specific electrophysiological responses of *Pieris brassicae* to individual glucosinolates (Schoonhoven, 1967) and laboratory behavioral tests of insect ability to discriminate among glucosinolates (e.g. Hovanitz and Chang, 1963; Hicks, 1974) suggest that *Pieris* and other crucifer specialists may distinguish among various Cruciferae (and other glucosinolate-bearing taxa) on the basis of this chemical class of more than 70 compounds (Ettliger and Kjaer, 1968; Rodman, 1978). In this paper I present evidence that *Pieris* preferences among several co-occurring crucifer species in a community are correlated with the presence of specific glucosinolates in these species. These results suggest that by affecting the intensity of *Pieris* herbivory on their allelochemically-similar neighbors, individual crucifer species may influence each other's evolution.

How do *Pieris* choose foodplants among allelochemically-similar taxa in a community? Chew (1974, 1975, 1977) characterized the behavioral and growth responses of a population of *Pieris napi macdunnoughii* to Crucif-

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erae in its montane habitat (Table 1). *P. n. macdunnoughii* responses to the native crucifer taxa in this community comprise three categories: a) a preferred foodplant, *Descurainia richardsonii* (nomenclature follows Weber, 1976) which supports significantly faster larval development to pupation than other native foodplants; b) a group of foodplants which support similar larval growth rates and among which adults and larvae show no consistent preferences, viz., *Arabis drummondii*, *Cardamine cordifolia*, *Draba aurea*, and *Thlaspi montanum*; and c) a crucifer which is unconditionally rejected by both ovipositing adults and feeding larvae—*Erysimum asperum*. The behavioral responses of *P. n. macdunnoughii* adults and larvae to these crucifers are thus consistent with each other: larvae are able to complete larval development on all crucifer species chosen by ovipositing females. In contrast, behavioral and growth responses of *P. n. macdunnoughii* to the naturalized weed *Thlaspi arvense* are inconsistent with each other: females accept *T. arvense* as an oviposition substrate and larvae feed on the plant, but die before completing development. Similar incongruity between female oviposition behavior and larval growth responses has been observed in a variety of Lepidoptera exposed to previously unencountered relatives of their foodplants (e.g. Straatman, 1962; Sevastopulo, 1964; Bowden, 1971). This inconsistency also characterizes the behavioral and growth responses of *Pieris occidentalis*, another native Colorado species, toward *T. arvense*. *P. occidentalis* places significantly fewer eggs on *T. arvense* than on native crucifers (Chew, 1977); however, unlike *P. n. macdunnoughii* avoidance of *Erysimum asperum*, *P. occidentalis* avoidance of *T. arvense* is statistical rather than absolute, with the result that substantial numbers of *Pieris* eggs are placed on this lethal plant. Since *T. arvense* is naturalized to this region, perhaps insufficient time has elapsed for the resolution of this incongruity. Botanical surveys of this region (see Chew, 1977) suggest that *T. arvense* has been abundant in this community for less than 100 years. Given the present pattern of behavior and mortality on *T. arvense*, *P. n. macdunnoughii* and *P. occidentalis* should eventually reject *T. arvense* plants as oviposition sites; alternatively, because females currently oviposit on *T. arvense* and larvae feed on the plant before dying (Chew, 1975), selection may favor any change which permits larvae to develop successfully on this plant.

Examination of the leaf glucosinolate profiles of these crucifer species shows that this community contains three distinct glucosinolate arrays (Table 2). The group of four species (in which *P. n. macdunnoughii* exhibits no consistent preference) is characterized by isopropyl glucosinolate and several biosynthetically related compounds. The unconditionally rejected plant, *Erysimum asperum*, contains methylsulfanylalkyl and methylsulfonylalkyl compounds, which are distinct from other major components of other glucosinolate profiles. Since some plants in this genus and the related

Table 1. Growth and behavioral responses of *Pieris napi macdunnoughii* to crucifer species growing in a montane Colorado community. These species include all locally abundant taxa which contain glucosinolates. Data are summarized from Chew (1974, 1975, 1977).

| Crucifer species | Oviposition | Feeding | Growth to pupation |
|-------------------------------------|-------------|---------|--------------------|
| (a) <i>Descurainia richardsonii</i> | Prefer | Prefer | Fastest |
| (b) <i>Arabis drummondii</i> | Yes | Yes | Yes |
| <i>Cardamine cordifolia</i> | Yes | Yes | Yes |
| <i>Draba aurea</i> | Yes | Yes | Yes |
| <i>Thlaspi montanum</i> | Yes | Yes | Yes |
| (c) <i>Erysimum asperum</i> | No | No | No |
| <i>Thlaspi arvense</i> ¹ | Yes | Yes | No |

¹ Naturalized from Eurasia.

genus *Cheiranthus* contain cardenolides (Hegnauer, 1964) *Erysimum asperum* may be chemically distinctive in this community on that basis as well; however, this species has not been examined for cardenolide content. The third array (with allylglucosinolate as a major component) includes both the preferred foodplant *Descurainia richardsonii* and the naturalized lethal crucifer *Thlaspi arvense*. Unlike the first two glucosinolate arrays, which correspond directly to crucifers in two behavioral-growth response categories, this third array comprises two crucifers whose effects on these *Pieris* are widely divergent.

The correlation of glucosinolate profiles with *Pieris* larval and adult behavior suggests that *P. n. macdunnoughii* distinguish among these crucifers at least partly on the basis of their glucosinolate profiles. In the case of *Erysimum asperum*, lack of information on the possible cardenolide content of this species precludes determination of what allelochemic class(es) mediates rejection of this plant by *Pieris* (Nielsen, 1978). While the possible physiological effects of individual glucosinolates on adapted crucivores such as *Pieris* have only begun to be explored (e.g. Marsh and Rothschild, 1974; Aplin et al., 1975; Blau et al., 1978), *Pieris* behavior towards *T. arvense* suggests that allylglucosinolate is perceived as a signal of suitable larval food. The allyl compound, and other major components of these glucosinolate profiles, are probably not intrinsic indicators of foodplant suitability for larval *Pieris*. Rather, *Pieris* behavior toward specific individual glucosinolates shared by several taxa probably depends on the evolutionary association of those glucosinolates with food resources of a particular quality. For these Colorado *Pieris*, it is likely that the consistent association of allylglucosinolate with the foodplant *Descurainia richardsonii* has been dis-

Table 2. Results of qualitative analysis of crucifer leaves for glucosinolates. Paper and gas-chromatographic methods are outlined by Rodman (1974). Data are summarized from unpublished data of Rodman and Chew.

| Crucifer species | Major glucosinolates (aglycone moiety) | Minor glucosinolates (number only) |
|--|--|------------------------------------|
| I. <i>Arabis drummondii</i> ¹ | Isopropyl-, 2-hydroxyisopropyl-, 2-butyl- | 5 |
| <i>Cardamine cordifolia</i> | Isopropyl-, 2-hydroxyisopropyl-, 2-butyl-, 1-ethyl-2-hydroxyethyl- | 1 |
| <i>Draba aurea</i> | Isopropyl- | 2 |
| <i>Thlaspi montanum</i> | Isopropyl-, 2-butyl-, (p)-rhamnopyranosyloxybenzyl- | 1 |
| II. <i>Erysimum asperum</i> | 3-methylsulfinylpropyl-, 4-methylsulfonylbutyl | 0 |
| III. <i>Descurainia richardsonii</i> | Allyl-, 3-butenyl- | 5 |
| <i>Thlaspi arvense</i> | Allyl- | 2 |

¹ Roman numerals refer to crucifer arrays described in the text.

rupted by the relatively recent introduction of *Thlaspi arvense* to this community; ovipositing adults may be confusing the lethal *T. arvense* with its allelochemically-similar associate *D. richardsonii*.

These data suggest that variation among members of a single chemical class may be significant in modifying insect behavior toward plants which contain this chemical class (cf. Dethier, 1978). For glucosinolates, variation may occur in two ways. First, biosynthesis of the aglycone moiety of the glucosinolate may vary, giving rise, for example to the hydroxylated compounds found in *Arabis drummondii* and *Cardamine cordifolia*; variation in the number of methylene groups occurs in *Descurainia richardsonii*. These changes probably involve minor modifications of existing biosynthetic pathways (e.g. Chew and Rodman, 1979 and references therein). In this case it is probably significant that electrophysiological work on *Pieris brassicae* shows that the receptors of this crucivore are more sensitive to the glucosinolates tested than to their corresponding isothiocyanates (Schoonhoven, 1967). Alternatively, after biosynthesis, a single glucosinolate may generate different aglycone products upon enzymatic hydrolysis (Benn, 1977). Allylglucosinolate, for example, may give rise to allylisothiocyanate or its isomer allylthiocyanate; allylthiocyanate has been found as the major hydrolysis product of *T. arvense* by others (e.g. Gmelin and Virtanen, 1960) but preliminary tests of *T. arvense* from this montane community reveal

allylthiocyanate as the major product. Feeny and colleagues (Feeny et al., 1970; Feeny, 1977) have shown that allylthiocyanate is much less attractive to crucivorous chrysomelid beetles under field conditions than the corresponding isothiocyanate.

While the variation generated within each crucifer species will be largely constrained by existing biosynthetic pathways (cf. Atsatt and O'Dowd, 1976), the adaptive value of a particular glucosinolate variant in a particular crucifer species depends on its relation to glucosinolates already present in the community (Jones, 1968; Dolinger et al., 1973; Janzen, 1973; Atsatt and O'Dowd, 1976; Cates and Rhoades, 1977; Feeny, 1977, Moore, 1978b). *Pieris* response to a novel compound in the glucosinolate profile of a particular crucifer will thus depend a) on whether it mimics the glucosinolate profile already produced by some other community associate (cf. Macior, 1970); b) on *Pieris* growth responses to species containing that glucosinolate; and c) on whether *Pieris* distinguish the plant containing the new glucosinolate from chemically-similar taxa in the community. To the extent that glucosinolates mediate the responses of *Pieris* towards their foodplants and to the extent that *Pieris* activity imposes differential mortality on different chemical morphs within crucifer populations (Jones, 1971; cf. Moore, 1978a; Morrow and LaMarche, 1978), it seems likely that these crucifer species evolve in relation to each other as well as in relation to the crucivorous *Pieris* in this community.

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Department of Biology, Tufts University, Medford, Massachusetts 02155.

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